

Ovaries, Ovarioles, and Oocytes in Parasitic Bees (Hymenoptera: Apoidea)

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Abstract.—Ovarian features of parasitic bees including the number of ovarioles per ovary, the number and size of mature oocytes, and the morphology of mature oocytes are explored. Included are data from 44 species representing approximately 8 separately derived cleptoparasitic lineages within the Apoidea. The number of ovarioles of parasitic Halictidae and Megachilidae is 3 per ovary, as is characteristic of non-parasitic Colletidae, Andrenidae, Halictidae, Melittidae, and Megachilidae. In the anthophorid/apid lineage, which has 4 ovarioles per ovary as a plesiomorphic condition, the Nomadinae tend to have increased numbers of ovarioles, with 5 ovarioles per ovary seeming to be the most common condition. In two other parasitic lineages of the Anthophoridae (Melectini and Ctenioschelini), only *Ericrocis lata* with 5 ovarioles has an increase from the plesiomorphic state. In the Apidae, *Psithyrus* consistently exhibits an above normal number of ovarioles.

Cleptoparasitic bees in all families tend to have a larger number of mature oocytes in their ovaries at a given time than do solitary bees, and these oocytes tend to be smaller than are those of solitary bees. Mature oocytes of the Nomadinae show considerable variation in structure from one another and from the oocytes of non-nomadine bees, as illustrated by *Nomada*, *Ammobates* and *Triepeolus*.

INTRODUCTION

Rozen (1986a) published a survey of the number of ovarioles in various taxa of bees, and realized, as had Iwata (1955, 1960, 1964, 1965) and Iwata and Sakagami (1966) before, that the number of ovarioles and other ovarian characteristics of bees have phylogenetic, taxonomic and adaptive significance. Cleptoparasitic bees especially seem replete with variable ovarian features. The works of these authors suggested that interesting patterns of variation exist from one parasitic lineage to another and that at least some of the variation may be explained in terms of the mode of life of the bees. To explore these matters more broadly, we collected, preserved in fixative and examined as many additional parasitic taxa as possible. Using both recently collected specimens and information from the literature, this paper reports on the number of ovarioles of different cleptoparasitic lineages, on the number and size of their mature oocytes and on other aspects of the morphology of the oocytes of the Nomadinae.

With great pleasure we dedicate this article to Dr. E. Gorton Linsley, one of the great systematists of cleptoparasitic bees (as well as many other groups of insects). The second author remembers with fondness being required to undertake the life

history study of one species of bee as part of his dissertation research by his major professor, Gort Linsley. This simple requirement led the second author to 35 years of digging holes both shallow and deep in most of the continents of the world in search of biological data about, and immature stages of, solitary and parasitic bees. Gort Linsley more than anyone else taught him that the data base for systematics was far greater than the specimen on a pin.

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MATERIALS AND METHODS

Original observations reported in this paper are based upon dissections of specimens that either were fixed and preserved in Kahle's solution prior to dissection (*Epeolus zonatus* from the Cornell collection and all of the AMNH specimens except *Triepeolus sp. R*) or were dissected as freshly killed specimens and subsequently fixed in Kahle's solution (all other Cornell material). The internal organs of specimens that have been preserved prior to dissection are somewhat brittle and more difficult to dissect without damaging structures one wishes to observe. New material reported in this paper deals with 25 species in 16 genera and 3 families of cleptoparasitic bees.

Because we compare our observations with the large data set previously gathered by Iwata (1955, 1960, 1965) and Iwata and Sakagami (1966), we use their definitions of stages of oocyte development and their measurement of body size. We repeat the definitions of their terms used in this paper: (1) EGG LENGTH (E) is the length (to the nearest 0.1 mm) of "the largest oocyte in the ovaries"; (2) MESOSOMAL WIDTH (M) is the "distance between the outer extremities of the tegulae" (mean value if more than one specimen was available); (3) EGG INDEX is the ratio E/M; and (4) MATURE OOCYTES are all oocytes in Iwata's (1955) categories A or B, defined as follows:

Category A: "mature oocytes, the nutritive cells of which have quite disappeared. In certain species the mature oocytes diminish their sizes a little to take their proper shapes."

Category B: "nearly mature oocytes, the nutritive cells of which begin to collapse. Generally they attain the maximum size proper to each species, but have not yet taken their proper shapes."

We count all oocytes tallied by Iwata as category A or B as mature oocytes because we were not confident that we could reliably distinguish between the two categories in our specimens. (Iwata worked primarily with fresh rather than preserved material, and his definitions of four discrete categories of developing oocytes were formulated in the framework of a survey of the oocytes of all Hymenoptera, rather than bees alone. The distinctions may be more apparent and significant in other Hymenoptera than they are in bees.)

The statistical tests used in this paper to analyze the number of mature oocytes in parasitic bees are Mann-Whitney U Tests (where sample sizes are adequate, P-values are based upon a standardized normal distribution of the U statistic). A

non-parametric statistical test is used because distributions are decidedly non-normal. Data for solitary species are all from Iwata (1955, 1960, 1965) or Iwata and Sakagami (1966). Data for parasitic species are from Iwata (13 species) and the present study (18 species).

RESULTS

Number of ovarioles.—In most families of bees (Colletidae, Andrenidae, Halictidae, Melittidae, and Megachilidae; unknown for the Stenotritidae, Oxaeidae, and Ctenoplectridae), there are 3 ovarioles per ovary (indicated by the notation 3:3 in Table 1), regardless of whether the bees are solitary, parasitic, subsocial, or social (Iwata and Sakagami, 1966; Rozen, 1986a). The present study corroborates this pattern for cleptoparasitic species in the Halictidae and Megachilidae (no cleptoparasitic bees in the other families for which data are available) (Table 1). In the Anthophoridae and Apidae, the presumed plesiomorphic condition is 4 ovarioles per ovary (i.e., 4:4 in Table 1). A notable exception is the subfamily Nomadinae, all of whose members are cleptoparasitic. Ovariole number appears to be more variable within the Nomadinae than in most other bees. It differs not only from species to species, but among individuals within a species, and sometimes even between ovaries within an individual (Table 1). Despite this variability, the number of ovarioles is almost always higher than the common anthophorid/apid condition of 4:4, and within the Nomadine 5:5 seems to be the most common condition.

We have examined four species of cleptoparasitic anthophorids that are not in the subfamily Nomadinae. Three species have the common anthophorid condition of 4 ovarioles per ovary, but *Ericrocis lata* has 5 ovarioles per ovary (Table 1).

Within the Apidae, an increase in ovariole number has been reported in five species of the socially parasitic genus *Psithyrus* (Cumber, 1949). The exact number of ovarioles is extremely variable, ranging from 6 to 18 per ovary (Table 1). By contrast, *Bombus*, the presumed sister group of *Psithyrus*, possesses the plesiomorphic number 4. (Queens in the related advanced eusocial genus *Apis* are remarkable among bees for their large number of ovarioles. Snodgrass (1956) estimated that *Apis mellifera* queens have 160 to 180 ovarioles per ovary.)

The fact that both *Psithyrus* and *Ericrocis lata* have more than 4 ovarioles (the plesiomorphic anthophorid/apid number) suggests that selection pressure for increased number of ovarioles has independently played a role in three separate groups in the anthophorid/apid line. We suspect, as did Iwata (1955, 1964) and Iwata and Sakagami (1966), that increased number of ovarioles functions to increase the total number of eggs that an individual can deposit. It also permits a greater number of mature oocytes to be ready for deposition within a short time period as pointed out below.

Number of mature oocytes.—Cleptoparasitic bees in all families tend to have a larger number of mature oocytes in their ovaries at a given time than do solitary bees. The difference is statistically significant, whether one tallies the total number of mature oocytes or the number of mature oocytes per ovariole (Table 2). The pattern also holds up if one divides the cleptoparasitic species into two subgroups on the basis of whether they have the same number of ovarioles as their non-parasitic relatives or an increased number of ovarioles. In comparing these two subgroups, we find that those species with an increased number of ovarioles have a significantly higher total

Table 1. Number of ovarioles and size and number of mature oocytes in various taxa of cleptoparasitic bees. Definitions of terms and notations are given in the text.

Taxon	Egg Index	Total Number Mature Oocytes	Mature Oocytes per Ovariole	Number of Ovarioles	Number of Specimens Examined	Reference
Halictidae						
<i>Sphecodes esakii</i>	0.36	9	1.50	3:3 ^a	2	Iwata, 1955
<i>Sphecodes japonica</i>	—	4	0.67	3:3 ^a	2	Iwata, 1955
<i>Sphecodes sp. A</i>	0.57	6	1.00	3:3	1	present study
<i>Sphecodes sp. B</i>	0.76	—	—	3:3	1	present study
Megachilidae						
<i>Dioxys pacificus</i>	0.74	2	0.33	3:3	2	present study
<i>Stelis sp.</i>	0.61	2.67	0.44	3:3	3	present study
<i>Euaspidis basalis</i>	0.53	3.5	0.58	3:3 ^{a,c}	3	Iwata, 1955, 1960
<i>Coelioxys (Rhinocoelioxys) sp.</i>	0.41	—	—	prob. 3:3	1	present study
<i>Coelioxys yanonis</i>	—	2	0.33	3:3 ^a	1	Iwata, 1955
<i>Coelioxys fenestratus</i>	0.54	18	3.00	3:3 ^a	1	Iwata, 1955
<i>Coelioxys brevis</i>	0.40	5	0.83	3:3 ^a	1	Iwata, 1955
<i>Coelioxys sp. (138)</i>	—	9	1.50	3:3 ^a	1	Iwata, 1955
<i>Coelioxys decipiens</i>	—	4	0.67	prob. 3:3 ^b	1	Iwata, 1965
Anthophoridae						
Anthophorinae						
<i>Thyreus japonicus</i>	0.85	3.5	0.438	4:4	2	Iwata, 1955
<i>Zacosmia maculata desertorum</i>	0.74	6	0.75	4:4	1	present study
<i>Mesoplia prob. rufipes</i>	0.74	4	0.50	4:4	1	present study
<i>Ericrocis lata</i>	0.77	2	0.20	5:5	1	present study
Anthophoridae						
Nomadinae						
<i>Neolarra (Neolarra) californica</i>	0.33	13.75	1.325	5:5 5:6	3 1	present study present study
<i>Neolarra (Neolarra) sp.</i>	—	—	—	5:5 (or 5:4)	1	present study
<i>Neolarra (Phileremulus) vigilans</i>	—	11	1.10	5:5	1	present study
<i>Holcopasites calliopsidis</i>	—	—	—	5:6	1	present study
<i>Ammobates carinatus</i>	0.47	6	0.50	6:6	1	present study
<i>Oreopasites sp. A</i>	0.49	7	0.74	5:4 5:5 (or 6:4)	1 1	present study present study
<i>Oreopasites vanduzeei</i>	—	—	—	approx. 11 total prob. 5:5	1 1	Rozen, 1986a Rozen, 1986a
<i>Kelita chilensis</i>	0.30	7	0.70	prob. 5:5 5:5	1 1	Rozen, 1986a present study
<i>Epeolus zonatus</i>	0.53	8.5	0.85	5:5	2	present study
<i>Epeolus scutellaris</i>	0.76	6.33	0.45	7:7	4	present study
<i>Epeolus sp.</i>	0.56	4	0.40	5:5	1	present study
<i>Epeolus japonicus</i>	1.00	6.5	0.54	6:6	2	Iwata, 1955
<i>Triepeolus pectoralis</i>	0.62	5	0.50	5:5	1	present study

continued

Table 1. continued

Taxon	Egg Index	Total Number Mature Oocytes	Mature Oocytes per Ovariole	Number of Ovarioles	Number of Specimens Examined	Reference
<i>Triepeolus sp. R</i>	0.49	2	0.20	5:5	1	present study
<i>Centrias articulata</i>	0.28	—	—	5:5	3	present study
<i>Nomada banksi</i>	0.30	15.5	1.55	5:5	3	present study
<i>Nomada vicina</i>	0.39	8	0.80	5:5	1	present study
<i>Nomada illinoiensis</i>	—	—	—	5:4	1	present study
				5:5	1	present study
<i>Nomada</i> ("Gnathias") <i>sp.</i>	—	—	—	5:5	1	present study
<i>Nomada pyrifera</i>	0.50	14.5	1.45	5:5	2	Iwata, 1955
<i>Nomada sp. nr. glabella</i>	0.38	8.67	0.90	5:5	2	Iwata, 1955
				5:4	1	Iwata, 1955
<i>Nomada japonica</i>	0.39	21.125	2.15	5:5	6	Iwata, 1955
				4:4	1	Iwata, 1955
				6:5	1	Iwata, 1955
Apidae						
<i>Psithyrus barbutellus</i>	—	—	—	10:10	1	Cumber, 1949
				10:12	1	Cumber, 1949
				6:7	1	Cumber, 1949
				8:9	1	Cumber, 1949
<i>Psithyrus bohemicus</i>	—	—	—	14:13	1	Cumber, 1949
<i>Psithyrus campestris</i>	—	—	—	7:8	1	Cumber, 1949
				6:7	1	Cumber, 1949
<i>Psithyrus rupestris</i>	—	—	—	18:15	1	Cumber, 1949
				15:13	2	Cumber, 1949
				16:14	1	Cumber, 1949
				12:14	1	Cumber, 1949
<i>Psithyrus vestalis</i>	—	—	—	10:10	1	Cumber, 1949

^aSpecies included in Iwata's Table IV (A), comprising "Anthophila with three pairs of ovarioles."

^bIwata's Fig. 50 shows a single ovary which clearly has only 3 ovarioles.

^cIwata (1960) explicitly lists number of ovarioles (for a single specimen) as 3:3.

number of mature oocytes, but they do not produce more oocytes per ovariole (Table 2).

Hence different lineages of parasitic bees have independently undergone an increase in the number of mature oocytes in their ovaries at a given time. This may reflect that parasitic bees produce more eggs in their life span than do solitary bees and that as a result a larger number of eggs are ready for deposit in a short interval. However, it is also likely that there is selective advantage for parasitic bees to be able to oviposit in rapid succession. Unlike a female solitary bee that must construct and provision a cell before each oviposition, a female cleptoparasite may find, and therefore must be ready to lay eggs in, more than one host cell in a short time period.

Size of mature oocytes.—Iwata and Sakagami (1966) reported that the mature

Table 2. Comparison of numbers of mature oocytes in parasitic vs. solitary bees.

	Total Number of Mature Oocytes	Mature Oocytes per Ovariole	Sample Size
1) Solitary Bees	2.17	0.34	26
	$U_s = 320$ $Z = 3.913$ $P < 0.001$	$U_s = 725$ $Z = 5.16$ $P < 0.001$	$U_s = 678.5$ $Z = 4.41$ $P < 0.01$
2) Cleptoparasitic Bees	7.18	0.86	31
a) With Unchanged Number of Ovarioles	5.62	0.90	14
	$U_s = 170$ $Z = 2.02$ $P < 0.05$	$U_s = 124$ $Z = 0.198$ $P = 0.84$	
b) With Increased Number of Ovarioles	8.46	0.84	17

oocytes of cleptoparasitic bees tend to be smaller than those of solitary species. Our observations corroborate this pattern, as shown in Figure 1 (which combines data from the present study and Iwata and Sakagami's study). It also appears that the distribution of egg sizes is relatively symmetrical in solitary species but decidedly asymmetrical and weighted toward smaller egg sizes in cleptoparasitic bees.

The egg index proposed by Iwata and Sakagami is a measure of oocyte size relative to overall body size. They suggested such a measure because they expected that oocyte size would vary with body size in a regular manner. Indeed, when maximum oocyte length is plotted against mesosomal width, both parasitic and non-parasitic species show a positive linear relationship between the two variables (Fig. 2. $r^2 = .758$ for parasites; $r^2 = .748$ for solitary species). Within the lower ranges of body sizes, parasitic species of a given size seem consistently to have smaller oocytes than solitary species of the same size. Such a trend is not apparent among larger bees in our sample.

Morphology of oocytes of the Nomadinae.—As has been noted by others (Iwata, 1960; Rozen, 1986a), mature oocytes of Nomadinae show remarkable variation in structure from one another and from the oocytes of non-nomadine bees. Figures 3–5 illustrate the oocyte features of some of the bees that we examined. The nipple-like structure on the anterior end of the oocyte of *Nomada vicina* (Fig. 3) was found also on two other *Nomada* seen by us but not on a fourth species; Iwata (1960) depicted nipples in two of the three species he studied. We presume that the corrugations that predominate on one side of the oocytes of *Ammobates* (Fig. 4) and *Oreopasites* (Rozen, 1986a, Fig. 1) permit the eggs to bend U-shaped as they are inserted into the cell walls of the hosts, as seems characteristic of the Ammobatini (Rozen, 1986b) with the exception of *Pseudodichroa* (Rozen and Michener, 1968). The completely annular corrugations of *Triepeolus pectoralis* oocytes (Fig. 5) and of the eggs of some other species in the same genus (Bohart, 1966) may allow for the expansion of the egg as it absorbs water in the cell wall of the host. We believe that oocytes of other

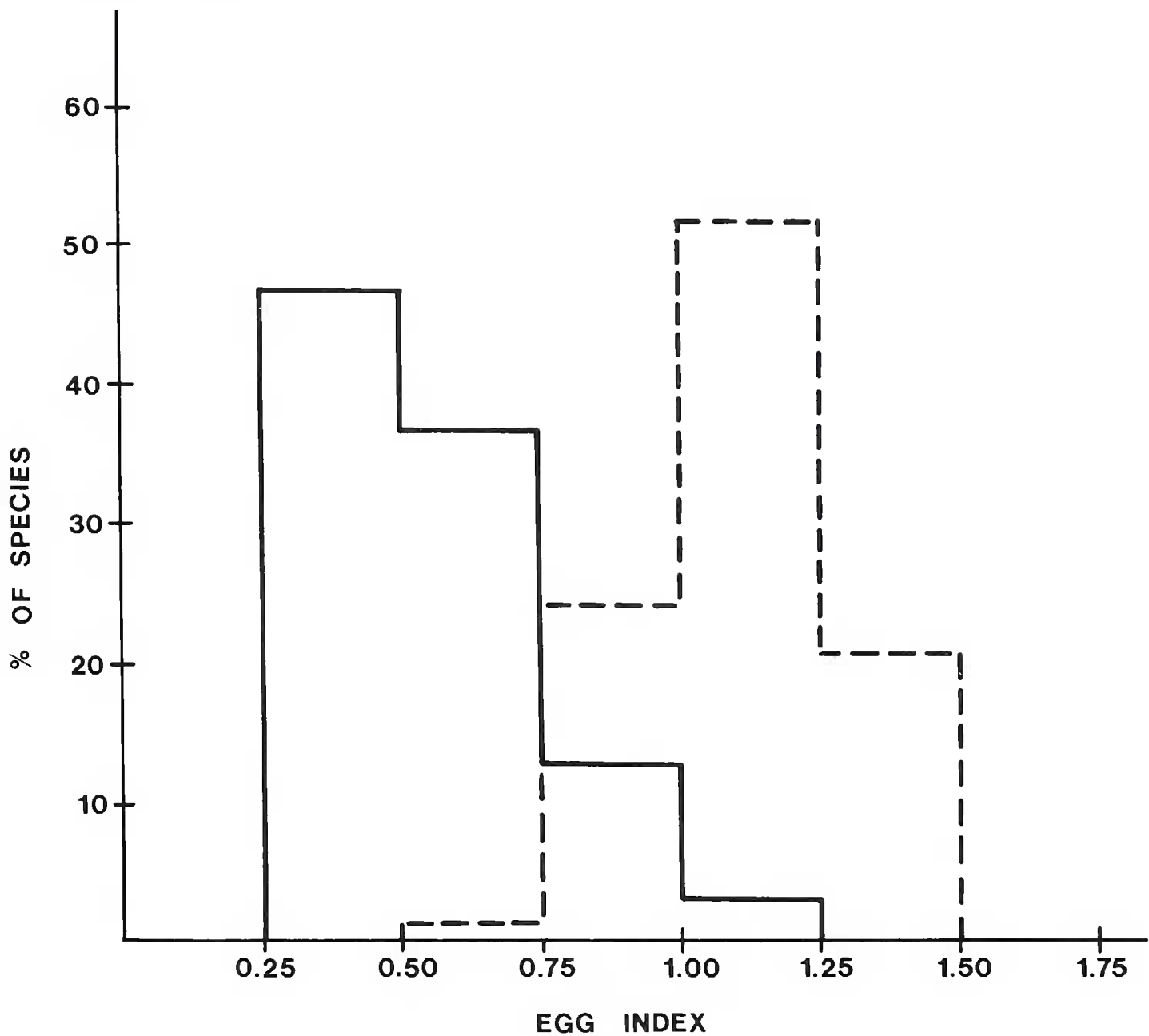


Figure 1. Frequency distributions for oocyte size (expressed as the EGG INDEX, or ratio of length of mature oocyte to mesosoma width) in cleptoparasitic bees (solid line) and solitary bees (dashed line).

Nomadinae will also be distinctive in shape and that shape will be correlated with the mode of oviposition of the taxon.

MATERIAL STUDIED

Sphcodes sp. A, 2 mi E of Apache, Cochise Co., Arizona, 9 May 1986 (J. G. Rozen). *Sphcodes sp. B*, 3 mi SW of Rodeo, Hidalgo Co., New Mexico, 5 May 1965 (J. G. Rozen). *Dioxys pacificus* Cockerell, 2 mi E of Apache, Cochise Co., Arizona, 9 May 1986 (J. G. Rozen). *Stelis sp. A*, Cienega Ranch, Hidalgo Co., New Mexico, 13 May 1986 (J. G. Rozen). *Coelioxys (Rhinocoelioxys) sp.*, near Chetumal, Quintana Roo, MEXICO, 12 October 1986 (G. C. Eickwort). *Zacosmia maculata desertorum* Cockerell, 2 mi E of Apache, Cochise Co., Arizona, 9 May 1986 (J. G. Rozen). *Ericrocis lata* (Cresson), 1 mi E of Douglas, Cochise Co., Arizona, 21 August 1986 (J. G. Rozen). *Mesoplia prob. rufipes* Perty, Hollis Reservoir, near Valencia, TRINIDAD, 3 March 1968 (J. G. Rozen). *Ammobates carinatus*

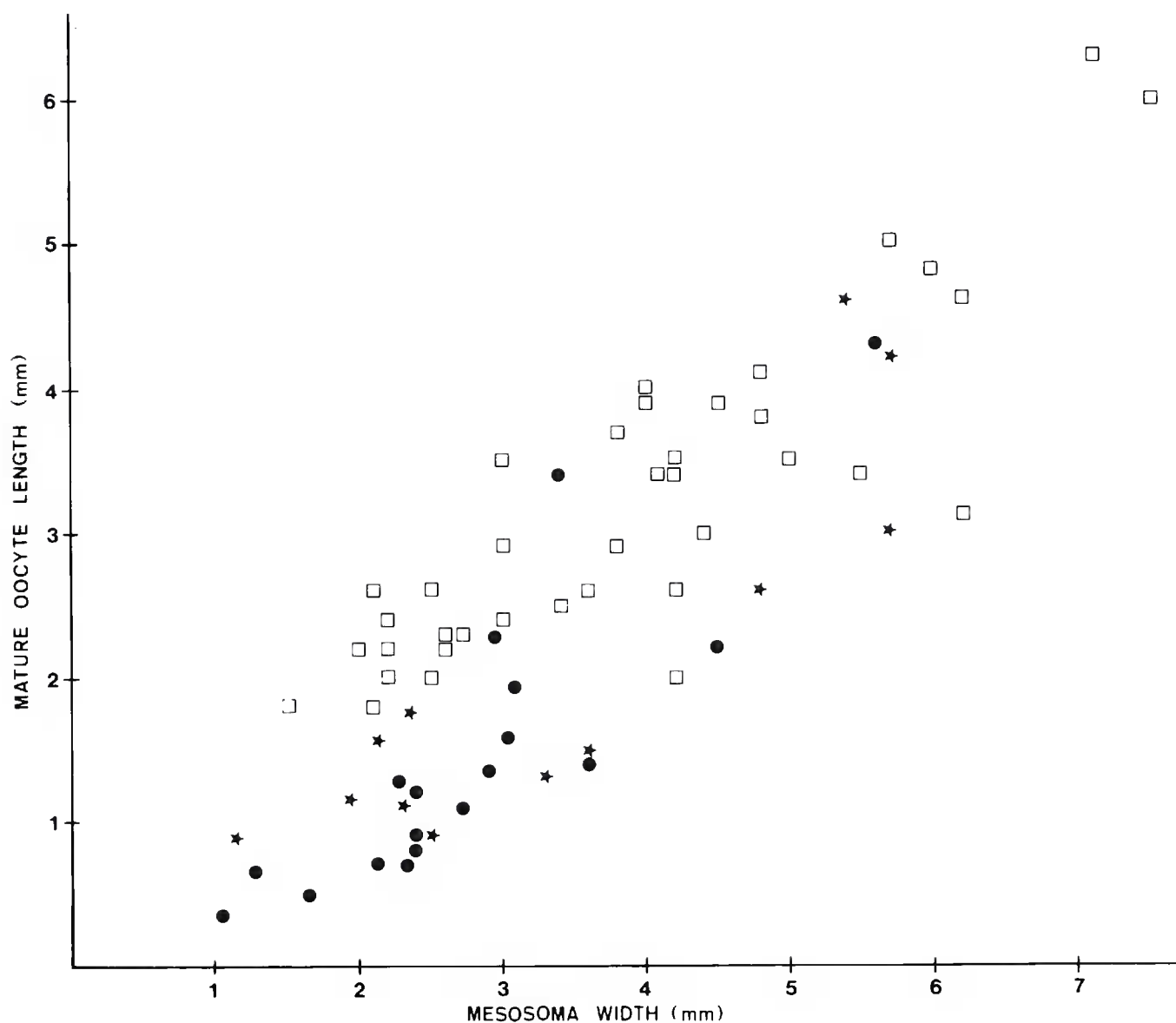


Figure 2. Scatter plot of mesosomal width versus length of mature oocytes in various species of bees. □ = solitary; ★ = cleptoparasites with same number of ovarioles as non-parasitic relatives; ● = cleptoparasites with increased number of ovarioles.

Morawitz, 10 km S of Skhirate, MOROCCO, 29 April 1968 (J. G. Rozen & E. Suissa). *Oreopasites sp. A*, 4 mi E of Willcox, Cochise Co., Arizona, 5 September 1986 (J. G. & B. L. Rozen), from nesting area of *Nomadopsis meliloti* (Cockerell). *Kelita chilensis* (Friese), Peñuelas, Valparaiso Prov., CHILE, 28 October 1969 (J. G. Rozen). *Triepeolus sp. R*, 11 mi S of Animas, Hidalgo Co., New Mexico, 20 August 1986 (J. G. Rozen). *Triepeolus pectoralis* (Robertson), Cornell Campus, Ithaca, Tompkins Co., New York, 3 September 1985 (B. Alexander). *Epeolus scutellaris* Say, Cornell Campus, Ithaca, Tompkins Co., New York, 1-5 September 1985 (B. Alexander). *Epeolus sp.*, 4 mi E of Willcox, Cochise Co., Arizona, 8 May 1986 (J. G. Rozen). *Holcopasites calliopsidis* (Linsley), Van Natta sand pit, Ithaca, Tompkins Co., New York, 11 July 1985 (B. Alexander). *Neolarra (Neolarra) californica* Michener, Cienega Ranch, Hidalgo Co., New Mexico, 10 May 1986 (J. G. Rozen). *Neolarra (Phileremulus) vigilans* (Cockerell), 19 mi SW of Apache, Cochise Co., Arizona, 29 August 1986 (J. G. & B. L. Rozen), from nesting site of *Perdita lenis* and *Perdita sp.*, *Neolarra (Neolarra) sp.*, 4.8 mi SW of Rodeo, Hidalgo

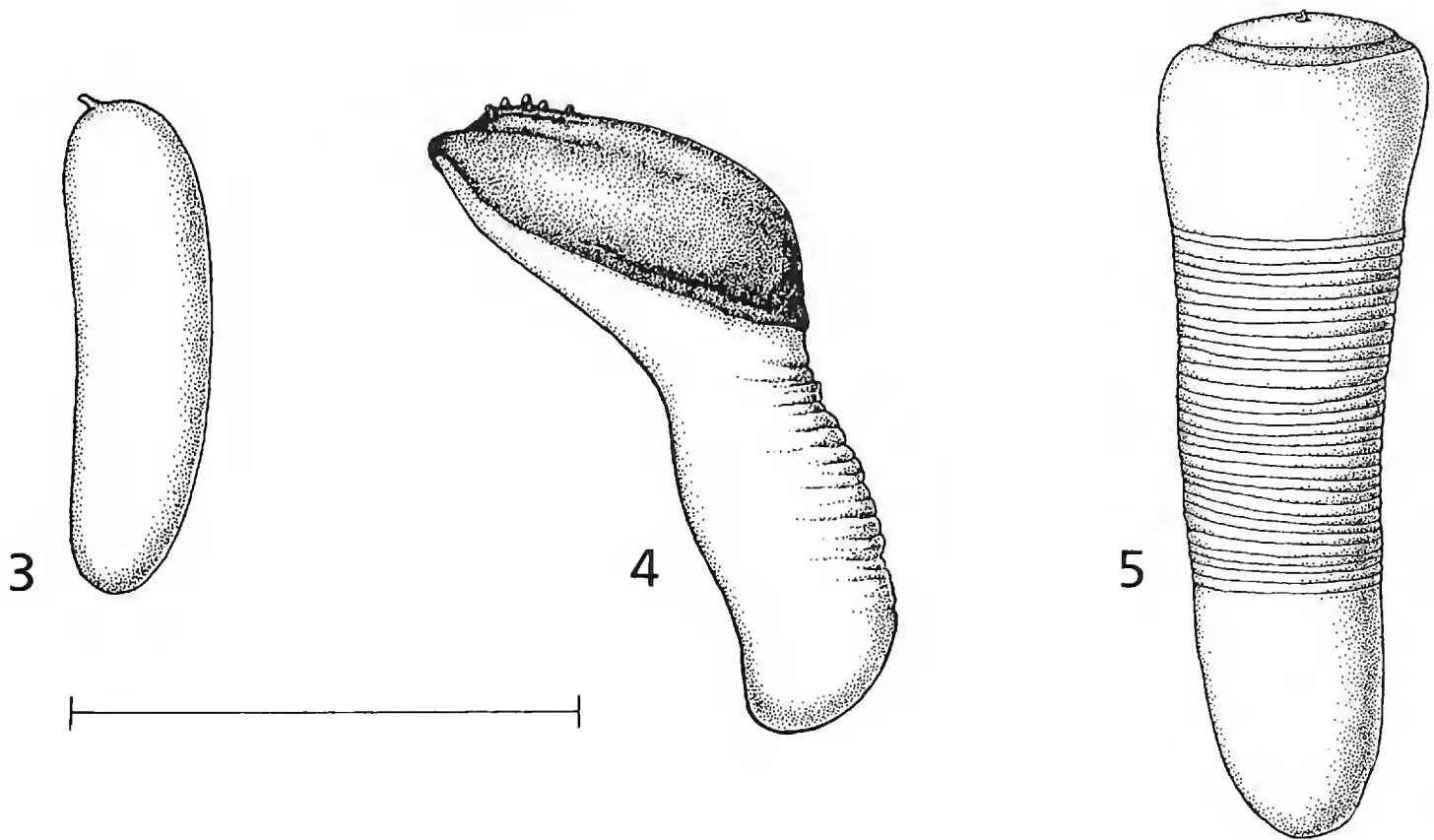


Figure 3-5. Mature oocytes of Nomadinae, anterior end at top. 3. *Nomada vicina*. 4. *Ammobates carinatus*. 5. *Triepeolus pectoralis*. Scale = 1.0 mm.

Co., New Mexico, 1 September 1975 (J. G. Rozen), from *Perdita mentzeliae* nest #7. *Centrias articulata* (Smith), Cornell campus, Ithaca, Tompkins Co., New York, 11 July 1985 (B. Alexander). *Nomada banksi* Cockerell, Van Natta sand pit, Ithaca, Tompkins Co., New York, 22, 29 September 1985 (B. Alexander). *Nomada vicina* Cresson, van Natta sand pit, Ithaca, Tompkins Co., New York, 23 September 1985 (B. Alexander). *Nomada* sp. (perhaps *illinoensis* Robertson), Cornell campus, Ithaca, Tompkins Co., New York, 15 May 1986 (B. Alexander). *Nomada* ("Gnathias") sp., near Junius Ponds, 6 mi NW of Waterloo, Seneca Co., New York, 18 May 1986 (B. Alexander).

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